

THE TAWNY MINING BEE, *ANDRENA FULVA* (MÜLLER) (HYMENOPTERA, ANDRENINAE), AT A SOUTH WALES FIELD SITE AND ITS ASSOCIATED ORGANISMS: HYMENOPTERA, DIPTERA, NEMATODA AND STREPSIPTERA

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Abstract The fossorial solitary bee *Andrena fulva* was studied at one of its nesting aggregations in Cardiff, South Wales, and rates of parasitism by its natural enemies (Hymenoptera, *Nomada panzeri*; Diptera, *Bombylius major*, *Leucophora obtusa*) were quantified over six years. This was done by placing nets over the previous year's nest entrances and collecting all host bee offspring and associated organisms as they first emerged in spring, and by dissecting host bees and their associated organisms. Cleptoparasitism by the cuckoo bee *N. panzeri* averaged 18% (ie 18% of *A. fulva* offspring were replaced by a *N. panzeri* offspring). Other natural enemies were seemingly of lesser prevalence (*B. major*: 3% parasitism; *L. obtusa*: 3% cleptoparasitism). Numerical sex ratios of host and parasites did not differ from 1:1. First instar exuviae of *Stylops melittae* were positively identified within the haemocoel of one *N. panzeri* female. This is the first report of any stage of a strepsipteran within a nomadiine bee. However, there was no evidence of *S. melittae* adults in either *A. fulva* or *N. panzeri*, suggesting that both bee species were inadequate hosts for *S. melittae* at this field site in S. Wales.

INTRODUCTION

Andrena comprises a large genus of ground-nesting bees with a primarily Holarctic distribution (Michener, 1979). Approximately 65 species of *Andrena* are found in Britain (Fitton *et al.*, 1978). Some of these are relatively common members of our spring fauna, though in a recent review over half of the British *Andrena* species were considered scarce or threatened (Falk, 1991). One member of the genus, *Andrena fulva* (Müller) (= *Andrena armata* (Gmelin)) (Hymenoptera, Andreninae), a harbinger of spring, may nest in dense aggregations in lawns of city parks and gardens in England and Wales (an aggregation existed up to the 1990s immediately in front of the Natural History Museum, London) as well as in Central Europe (e.g. Klausnitzer, 1976; Gusenleitner, 1985). A nesting female produces a characteristic miniature 'volcano' of soil, a tumulus, above its nest entrance (Fig. 1). Its nesting habits and locations, along with its deep red dorsal covering of hair, mean that *A. fulva* is commonly encountered and recognized.

Bees and their nests are known to host a wide range of associated insects, particularly from the orders Diptera, Coleoptera and Hymenoptera, some parasitic and others commensal (e.g. Batra, 1965; Paxton *et al.*, 1996). Yet, despite the abundance and accessibility to observation of *A. fulva*, surprisingly little has been reported on its biology and associated organisms (cf. Gusenleitner, 1985). It is known to be the sole host of the rare cleptoparasitic bee *Nomada signata* Jurine (Hymenoptera, Anthophorinae) (Westrich, 1989) and to be one of several hosts of



Fig. 1. An *Andrena fulva* female (wing length circa 10 mm) emerges from its tunnel entrance around which there is a tumulus or 'volcano' of soil, material that she has removed from her nest during its construction. Photo: RJP (with permission, IBRA).

another cleptoparasite bee, *Nomada panzeri* Lepeletier (Hymenoptera, Anthophorinae) (Richards, 1946; Gusenleitner, 1985).

Strepsiptera comprise an order of 550 plus described species that are entomophagous endoparasites, attacking members of the following taxa: Zygentoma, Mantodea, Blattodea, Ensifera, Caelifera, Sternorrhyncha, Auchenorrhyncha, Heteroptera, Hymenoptera, and Diptera (Kinzelbach, 1978; Kathirithamby, 1989). Though they have a worldwide distribution and have for long attracted the attention of entomologists, they remain an understudied and enigmatic group. Their sexual dimorphism is extreme. The winged, short-lived males have a bizarre appearance whilst females are larviform and neotenic, most species remaining embedded within the abdomen or gaster of their hosts. A strepsipteran larva has a planidial primary larval stage that subsequently develops as an internal parasite of the juvenile stages of a host (Kinzelbach, 1978; Kathirithamby, 1989). Species identification, particularly of females, is difficult. Even the taxonomic position of the order is unclear, and has been debated since its erection by Kirby in 1813. The group was earlier considered to be related to, even a part of, the Coleoptera (Crowson, 1981; Lawrence & Newton, 1995). Kristensen (1991) suggested that the Strepsiptera are not members of the Endopterygota; he placed them as "Neoptera incertae sedis". Molecular phylogenetic analyses have more recently suggested that the Strepsiptera and Diptera are sister clades and therefore probably more closely related (Chalwatzis *et al.*, 1996; Whiting *et al.*, 1997).

Members of the stylopid genus *Stylops* are parasites of bees of the genus *Andrena* (Kinzelbach, 1978). Though *Stylops* are only sporadically encountered, they can be locally common, and have been implicated in the demise of nesting aggregations of their *Andrena* hosts (Theobald, 1892). Given the difficulties of stylopid species identification, little is known of their host specificity, though it is clear that some *Stylops* species can parasitize more than one *Andrena* species (Bohart, 1936; Kinzelbach, 1978; Pohl & Melber, 1996). Differences in the proportions of the female cephalothoraces, in the shape of the aedeagi of the males, and in the first instar larvae indicate that *S. melittae* from the Western Palaearctic is not a homogenous species (Kinzelbach, 1978; Borchert, 1963; Pohl, 1998), though the precise species status of morphologically disparate specimens is not clear. For this reason, we follow Kinzelbach (1978), who synonymized all described *Stylops* species from the Western Palaearctic.

Our study was designed to document the organisms associated with *A. fulva* at one of its nesting aggregations in the suburbs of Cardiff, Glamorgan, S. Wales, and to quantify rates of parasitism of its natural enemies. During the study, first instar larval stages of *Stylops melittae* Kirby 1802 (Strepsiptera, Stylopidae) were encountered in *N. panzeri*, a cleptoparasite of *A. fulva*; this is the first report of any stage of a *Stylops* found within a nomadine bee.

MATERIAL AND METHODS

Andrena fulva nests are often aggregated in a spatially discrete area of apparently suitable ground and, though the species is univoltine, with adults living but a few weeks in spring, aggregations persist over many years (Gusenleitner, 1985). *Andrena fulva* was studied for six consecutive years (1988–1993) at one such aggregation in Cardiff (field site 'Heol Don', ST149797).

The life cycle of *A. fulva* is typical of other vernal *Andrena* species; adults overwinter underground within their natal cells then emerge in the following spring, males to mate and females to provision their own offspring with self-collected pollen and nectar (Westrich, 1989). Each female constructs her own brood cells at the end of her own self-dug tunnel into the ground. Bees were collected as they first emerged from their natal cells in spring using cages of fine nylon netting (emergence traps) placed over the entrances of the previous year's nests (Fig. 2). Offspring generally first emerge in spring through their natal tunnel rather than excavating a new gallery from their natal cell to the soil surface.

Emergence traps were put out over individual nests in spring, well before the emergence of any bees, and they were examined one or more times per day throughout the emergence and flight period. All host bees and any associated organisms emerging from *A. fulva* nests into emergence traps were recorded and either released immediately or returned to the laboratory for further study. Emergence trap data provide one means of quantifying rates of parasitism for those brood parasites that have a life cycle and spring emergence behaviour similar to those of their host. Little is known of the life cycle of some of the Diptera associated with *A. fulva* at Heol Don and their mode of egress from host cells and nests in spring. Therefore the use of emergence traps may give only an approximate estimate of the importance of these organisms as putative parasites of *A. fulva*.

All emerging bees were examined visually for the presence of Strepsiptera protruding through their gasters, namely female cephalothoraces or male puparia. Additionally, some males and females of both *A. fulva* and *N. panzeri* were dissected under insect saline and their gastral tissues examined with the aid of a binocular microscope ($\times 40$ magnification) for the presence of internal parasites, including

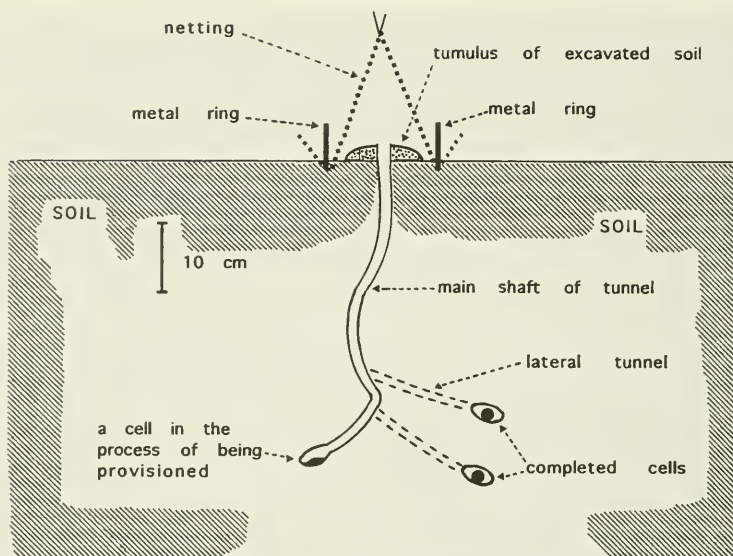


Fig. 2. Cross-sectional view of an *Andrena fulva* nest in spring with emergence trap *in situ* to collect all emerging offspring and associated organisms.

Strepsiptera. Other adults of *A. fulva* and *N. panzeri* were collected from Heol Don after emergence, visually inspected, and then dissected and also examined for parasites.

RESULTS AND DISCUSSION

The host bee, *Andrena fulva*

A total of 402 *A. fulva* was collected from emergence traps across the six years of their use at Heol Don, with a numerical sex ratio not significantly different from 1:1 ($\chi^2=0.020$, $df=1$, n.s.; Table 1). Generally, a non-biased sex investment ratio is

Table 1. Numbers of host *Andrena fulva* bees and their natural enemies collected from emergence traps across six years at Heol Don, Cardiff. The per cent parasitism by natural enemies assumes that one host bee is replaced by one enemy.

species	role	number of adults emerging			% parasitism
		females	males	unknown	
<i>Andrena fulva</i>	host bee	203	199	—	
<i>Nomada panzeri</i>	cleptoparasitic bee	44	51	—	17.9%
<i>Bombylus major</i>	parasitic fly	7	5	4	3.0%
<i>Leucophora obtusa</i>	cleptoparasitic fly	7	8	—	3.0%
<i>Brachicoma devia</i>	? parasitic fly	1	—	1	0.4%
<i>Fannia hamata</i>	? parasitic fly	—	1	—	0.2%

expected in solitary insects such as *A. fulva*, though the sex ratio varies from male-biased through to female-biased in other solitary bees (Crozier & Pamilo, 1996).

The cuckoo bee, *Nomada panzeri*

The cuckoo bee *N. panzeri* (Fig. 3) was abundant at Heol Don, where *A. fulva* represented its major host. It was often seen to enter burrows of *A. fulva*. *Nomada signata*, though found elsewhere in Cardiff (RJP, pers. obs.), was never encountered at Heol Don. Like its host, *N. panzeri* is univoltine and overwinters as an adult, ready to emerge in the following spring in the same fashion as its host, through the host mother's tunnel entrance. In addition to *A. fulva*, 95 *N. panzeri* were collected from emergence traps; the numerical sex ratio of the cuckoo bee at emergence was also not significantly different from 1:1 ($\chi^2=0.260$, $df=1$, n.s., Table 1).

One or more *Nomada* females lay eggs within host cells, only one of which survives to consume the host egg or larva and the provisions of pollen and nectar which its host mother had stored in its cell (Westrich, 1989). Thus one, and only one, *Nomada* offspring can develop within a host cell, always replacing the host offspring (Rozen, 1991). Assuming one individual of all other parasites collected in the emergence traps likewise replaced one host offspring, parasitism of *A. fulva* brood cells by *N. panzeri* can be calculated to have averaged out at 17.9% across the six years of study.



Fig. 3. A *Nomada panzeri* female (wing length circa 8 mm), a common cleptoparasitic bee of *Andrena fulva* at Heol Don, sits ominously over a tunnel of its host. Photo: RJP.

Though a well known cleptoparasite of *A. fulva* and other members of the genus *Andrena* (Richards, 1946), the rate of parasitism by *N. panzeri* has not previously been quantified. Clearly, cleptoparasitism by *N. panzeri* represents a considerable cost to its host, *A. fulva*, at Heol Don.

Dipteran associates

Female bee flies, *Bombylius major* Linnaeus (Diptera, Bombyliidae), were occasionally observed over the Heol Don nesting aggregation, hovering 5–15 cm above *A. fulva* nest entrances and flicking dust-covered eggs towards the ground with a bobbing motion of the apex of the abdomen. Such oviposition behaviour is typical of bee flies (e.g. Andrietti *et al.*, 1997; Stubbs, 1997), whose larvae (planidia) crawl to underground host bee cells where they consume host larvae or prepupae (Bohart *et al.*, 1960). *Bombylius major* is thought to be a parasite of numerous fossorial bee species (Askew, 1971). Empty exuviae of *B. major* were often found protruding above the soil surface within the nesting aggregation at Heol Don, suggesting that their owners had parasitised *A. fulva* cells beneath. Excavation of one *A. fulva* nest at Heol Don revealed two larvae of *B. major* within host cells, thus confirming this bee fly as a parasite of *A. fulva*. Interestingly, both bee flies required two years to reach adulthood, suggesting they may have a two- or multi-year life cycle, as also seems to be the case for *B. major* parasitizing *Andrena scotica* Perkins 1916 in Sweden (Paxton *et al.*, 1996).

Estimating the rate of parasitism by *B. major* of *A. fulva* has three complications. Firstly, it is not known whether just one host bee larva/prepupa suffices for the development of a bee fly or whether several are required (see Batra, 1965). Secondly, bee fly larvae make their exit from subterranean host cells not through the host mother's tunnel but more likely by burrowing vertically upwards through the soil immediately above a host cell using large proximal and distal spines (e.g. Bohart *et al.*, 1960). Thirdly, as suggested above, *B. major* most likely has a multi-year life cycle, a feature which may be common in temperate bombyliids (Bohart *et al.*, 1960). They are therefore unlikely to be captured within emergence traps placed over the previous year's host nests. The 3.0% parasitism of *A. fulva* offspring by *B. major* (Table 1) is therefore probably a large underestimate. Other bombyliids are considered to inflict greater brood mortality on their host bees (e.g. at least 5.8% for a halictid bee, Packer, 1988). The numerical sex ratio of *B. major* at emergence was not significantly different from 1:1 ($\chi^2 = 0.168$, df = 1, n.s.).

The satellite fly *Leucophora obtusa* (Zetterstedt) (Diptera: Anthomyiidae) was often encountered around the nesting aggregation of *A. fulva* at Heol Don, and it has been previously recorded following *A. fulva* in Britain (Copeman, 1921; described therein as *Hammomyia* (*Hylephila*) *unilineata* Zett.). At Heol Don, a female satellite fly would pursue a female *A. fulva* returning to its nest carrying pollen provisions, 'shadowing' the host bee in flight by a distance of approximately 5–10 cm until the host entered its nest. *Leucophora obtusa* then followed one of two approaches to gain access to the bee's nest and, presumably, to oviposit within it. Either it would immediately follow the host bee into its nest (Fig. 4), presumably to inspect the nest's contents, reverse out of the nest, then re-enter the nest in reverse, presumably to oviposit. Alternatively, it would sit motionless at 2–6 cm distance from the host nest, head pointed at its entrance. After approximately 20–30 minutes, the host bee usually re-emerged and flew away on another pollen or nectar provisioning flight, whereupon the satellite fly ran up to the host nest, inspected it and oviposited within it as described above.



Fig. 4. A female of the anthomyiid satellite fly *Leucophora obtusa* (wing length circa 5 mm) enters head first a tunnel of its host, *Andrena fulva*, at Heol Don, possibly to inspect its contents. Photo: RJP (with permission, *Entomologisk Tidskrift*).

Though other *Leucophora* species are known to 'shadow' other presumed host bee or wasp species, there is little information on their oviposition strategies with which to compare these observations of *L. obtusa* (see Paxton *et al.*, 1996). Certainly *L. obtusa* has been reported to parasitise several *Andrena* species (Hennig, 1976).

Satellite fly larvae eat the pollen mass with which host bee larvae have been provisioned (Hennig, 1976); they are cleptoparasites. *Leucophora obtusa* offspring probably emerge from overwintering through their host's tunnel and collect in emergence traps. Assuming *L. obtusa* has the same life cycle as that of *A. fulva*, its rate of parasitism was low at Heol Don, at an estimated 3.0% (Table 1). It is likely that more than one *L. obtusa* could have developed on the provision mass of one host bee cell (see Knerer & Atwood, 1967) and therefore the estimate of 3.0% may itself be an overestimate. For other bee species, *Leucophora* cleptoparasitism has been shown to be higher (e.g. 7.2% for one population of halictid bees in the USA, Eickwort *et al.*, 1996). The numerical sex ratio of *L. obtusa* at emergence was not significantly different from 1:1 ($\chi^2=0.125$, $df=1$, n.s.).

Two other fly species were collected in very low numbers from emergence traps (Table 1). *Brachicoma devia* Fallén (Diptera, Sarcophagidae) is a known parasite of bumble bee larvae (Alford, 1975). *Fannia hamata* Macquart (Diptera, Fanniidae) larvae are commensal in wasp (*Vespula* spp.) nests (Spradbery, 1973); other *Fannia* spp. larvae consume detritus in wasp and bumble bee nests (Spradbery, 1973; Alford, 1975). It is not clear whether these irregular associates of *A. fulva* nests were indeed parasites of the bee's brood.

Nematoda

Dissection of 159 female and 9 male *A. fulva* revealed 3 mermithid nematodes, one in each of three female bees. Mermithids are generalist parasites of soil-dwelling insects and have been previously recorded as parasites of other fossorial bees (Batra, 1965). No other organisms, such as diplogasterid nematodes (Giblin-Davis *et al.*, 1990; Erteld, 1995), were recorded in association with *A. fulva*.

Strepsiptera

All bees collected from emergence traps were without external signs of stylopisation. An additional 91 female and 73 male *A. fulva* and an additional 10 female and 11 male *N. panzeri*, collected as free-flying adults from around Heol Don, showed no external signs of stylopisation. During casual observation, other adults of *A. fulva* and *N. panzeri* were never seen with external signs of stylopids at Heol Don across the six years of study.

Dissection of 13 female and 6 male *N. panzeri* revealed 2–30 dark brown spheres approximately 1 mm³ in diameter within the gastral haemocoels of three of the females, each of which had been collected from Heol Don as a free-flying adult. Spheres were brittle and opaque so their contents could not be determined. Careful inspection by microscopy ($\times 400$ magnification) of brown flecks in the adipose tissue of one of the females containing dark spheres revealed the exuviae of two first instar larvae of *Stylops melittae* (Fig. 5), each approximately 0.23 mm in body length, and lacking any internal structures.

Only first instar exuviae of strepsipterans can be found in hosts because the second instar larva remains in its exuvia (Kathirithamby, 1989; H.P. pers. obs.). The encapsulation and melanisation of juvenile stage parasites by host insects is a well characterized immune response (Kraaijeveld & van Alphen, 1994). We hypothesize that the dark spheres that were found within *N. panzeri* haemocoels may represent encapsulated stylopids.

Though there are several cases of errant first instar larvae of Strepsiptera been found in non-specific hosts (e.g. in a first instar larva in an aphid, Prior, 1976; or in a phlebotomid, Rageau, 1951), this is the first report of any stage of a *Stylops* having been found inside an insect other than an *Andrena* host. Given the small size of styloid first instar larval exuviae and their location, embedded within gastral adipose tissue, it may be the case that stylopids in other dissected bees (*A. fulva*: 159 females, 9 males; *N. panzeri*: 10 other females, 9 males) were overlooked in this study.

How is it that exuviae of styloid first instar larvae were to be found inside *N. panzeri* adults? Primary larvae of *Stylops* are deposited onto flowers as host *Andrena* females, bearing a gravid *Stylops* female within their gasters, walk lethargically across blossoms (Linsley & MacSwain, 1957). *Stylops* larvae are assumed to climb onto other bees that subsequently visit the same flowers and are transported by them, possibly within the honey crop (Linsley & MacSwain, 1957; Batra, 1965). If the vector of the *Stylops* is a host female then, when the host bee is back at its nest, *Stylops* larvae climb onto or are deposited onto host provisions and subsequently enter the host egg or first instar larva to continue their own development (Linsley & MacSwain, 1957; Kathirithamby, 1989). For *S. melittae* to have been found within the haemocoelic tissue of *N. panzeri* adults implies that the styloid first instar larvae must have entered a *N. panzeri* larva, presumably soon after it had itself consumed the original *A. fulva* egg or larva within a brood cell.



Fig. 5. An empty exuvia of a *Stylops melittae* first instar larva within adipose tissue of an adult *Nomada panzeri*. Total length of exuvial cavity: 0.23 mm. The head capsule has become partially detached from the rest of the exuvia. Photo: HP.

Each *N. panzeri* carrying dark spheres, including the individual in which *S. melittae* first instar exuviae were positively identified, contained spermatozoa in its spermatheca and mature oocytes in its ovarioles, suggesting that all were reproductively active. Host *Andrena* bees containing mature *Stylops* females in their gasters are effectively sterile, mating but not producing mature oocytes nor provisioning cells within a nest (Smith & Hamm, 1914; Linsley & MacSwain, 1957). It appears that *N. panzeri* was an inadequate host for *S. melittae*.

British *A. fulva* have occasionally been recorded as having been successfully styloped by *S. melittae* (Perkins, 1892, 1918a,b; Kinzelbach, 1978). In Germany, *A. fulva* is also an often reported host of *S. melittae* (Ulrich, 1956; Borchert, 1963; Saure, 1994; Kuhlmann, 1998). Within Berlin, there is one supposed 'host race' of *S. melittae* which parasitizes only *Andrena vaga* Panzer (Borchert, 1963) despite the presence of *A. fulva* at the same location. At our Welsh field site, *S. melittae* parasitizes *A. scotica*, where hosts infected with female *S. melittae* visit the same blossoms as *A. fulva* females. That there was no evidence of *Stylops* imagines in *A. fulva* at Heol Don despite the existence of *S. melittae* within its cuckoo bee and in the local environment suggests that *A. fulva*, too, may be an inadequate host for this putative 'host race' of *S. melittae* at this field site. A considerable step forward in the systematics of *Stylops* species can only be made with greater series of males and first instar larvae derived from different host bees.

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